MYCORRHIZAE-PLANT RELATIONSHIPS

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Abstract. Greater than 80% of all plants are reported to form either ectotrophic or endotrophic mycorrhizal roots in a symbiotic association with fungi. This association modifies the biology of the plant and provides a beneficial effect by increasing nutrient uptake, deterring root pathogens and increasing plant resistance to environmental stress. The influence of the mycorrhizal associations will vary with the different fungal symbionts and as environmental conditions at different planting sites change. For these reasons, scientists and practicing nurserymen are now combining their efforts in an attempt to obtain maximum potential from selected manipulation of the mycorrhizal association.

A complex of divergent microorganisms (fungi, bacteria, actinomycetes, nematodes, etc.) is associated with all plant roots. This association varies from being extremely specific, exemplified by the legumes and the associated nitrogen fixing bacteria (*Rhizobia* sp.), to the relatively loose associations found in the rhizosphere where organisms appear to have no specific function, but are adapted to the unique soil environment created by the presence of the plant root.

The symbiotic association of fungi and plant roots results in the production of a root structure referred to as mycorrhiza ("fungus root"). Only a limited number of fungi can form this association, yet greater than 80% of all higher plants are believed to exist in this symbiotic association.

TYPES OF MYCORRHIZA

Ectotrophic mycorrhiza can be recognized by the swollen short roots, often richly branched, lacking root hairs and, as a rule, surrounded by a thick hyphal sheet. This hyphal sheet effectively isolates the root from direct contact with the soil. In this association, the fungal hyphae which enter the plant root, are intercellular only in the outer root cortex. Higher fungi, belonging to the Hymenomycetes and Gasteromycetes, are responsible for forming this association (18). The ectotrophic mycorrhiza are the type most frequently developed in association with coniferous forest vegetation. In the natural environment, nearly all feeder roots will be mycorrhizal.

Endotrophic mycorrhiza can be recognized by loose network of hyphae in the soil surrounding the root and by extensive hyphal growth within the root cortex. In the endotrophic mycorrhiza, the hyphae which enter the plant root are intracellular and are confined within the cortical tissue only by the digestive activity of the plant root cells. Lower phycomycetes are responsible for the

formation of endomycorrhiza. This is the most widespread mycorrhizal association and is of particular interest because of the large number of agricultural crops on which it occurs.

Ectendotrophic mycorrhiza are similar to the ectotrophic type but have both inter- and intracellular hyphae occurring in the root cortex. In this way, they are somewhat of an intermediate form to the previously described types.

There are differences in the life cycles of the fungi producing ectotrophic and endotrophic mycorrhizal roots which could have ramifications in nursery management practices. Fungi forming endomycorrhiza produce spore forming structures only within the soil matrix and do not produce aerial fruiting bodies, hence little or no distribution of material occurs by normal air currents. Fungi forming ectomycorrhiza do produce aerial fruiting bodies (the common mushroom) which release spores that may be transported over considerable distances by normal wind currents. Repeated sterilization of nursery soil will therefore restrict the potential for mycorrhiza formation to the ectomycorrhizal type. The re-introduction of infective particles will normally be limited to aerial transport unless corrective inoculation procedures are instituted.

MYCORRHIZAL INFLUENCE ON PLANTS

The mycorrhizal association modifies the biology of the plant root and consequently the whole plant, morphology, physiology and ecology. As a result of this modification, the mycorrhizal fungi benefit plants by a) aiding in the absorption of inorganic nutrients, b) deterring root pathogens and c) increasing host plant resistance to drought and extreme soil temperature.

(a) **Absorption of Inorganic Nutrients.** In the formation of the mycorrhizal root, the development of root hairs is suppressed. The fungal mycelium which produces a sheath around the rootlet and penetrates the root cortex functionally replaces the root hair. Growth of this mycelium into the soil provides an extension of the plant root system enabling it to exploit a greater soil volume and obtain the associated nutritional benefits (17). For this reason, it is logical to expect the greatest benefit from mycorrhizal association to occur under conditions of nutrient deficiency or with plants which do not have a vigorously branching fibrous root system. The beneficial nutritional effects have been demonstrated primarily for phosphorus (11) but have also been noted for nitrogen (19), sulfur (3) and several other elements (11). All the mycorrhizal fungi are not equally efficient in producing this effect. Table 1, taken from the work of Mejstrik and Krause (10), outlines the variable effect of two symbionts on the uptake of different phosphorus forms by radiata pine. From this, it appears that there are conditions under which it would be ecologically advantageous to establish specific mycorrhizal formers.

(b) Deterring Root Pathogens. Systematic investigations of the role of mycorrhizal roots as opposed to nonmycorrhizal roots in the resistance of plants to feeder root disease, have shown that mycorrhiza on plants decrease the incidence of feeder root disease (7). The description of the ectomycorrhiza noted that the hyphae isolated the root from the soil. This same hyphal sheath could therefore present a physical barrier to the invading root pathogen. In addition, the fungal symbiont could produce an antibiotic which inhibits pathogen development, or the fungal symbiont might induce the host to produce compounds toxic to the invading pathogen.

Table 1. The effect of different treatments upon absorption from different solutions (results expressed in relation to uptake by uninoculated controls).

Source of Phosphorus	Symbiosis	Total Uptake (%)
Resin - available phosphate (0.1 ppm)	No mycorrhiza	100
	Cenococcum graniforme	99
	Suillus luteus	147
Humus - organic phosphate in humus (0.58 ppm)	No mycorrhiza	100
	Cenococcum graniforme	194
	Suillus luteus	408
Nutrient solution with H_3PO_4 (7.2 ppm)	No mycorrhiza	100
	Cenococcum graniforme	87
	Suillus luteus	146

Both the fungal symbiont and the pathogen receive the organic compounds necessary for their growth from the host. Part of these are made available as root exudates, i.e. products which leak from the root as a result of the normal growth process. The presence of a mycorrhizal fungi utilizing the root exudates would make them unavailable for the growth of a pathogen. Another possible control mechanism could result from the selection of a unique population of organism around the mycorrhizal root (mycorrhizal rhizosphere) (13) which was antagonistic to the invading pathogen. In the soil system, probably no single mechanism is effective but control comes from a combination of several interacting processes. Table 2 (7) indicates the response that could be expected from this control.

Table 2. Growth of *Pinus echinata* with and without Ectomycorrhizae in the presence and absence of *Phytophthora cinnamoni*.

Measurements	Nonmycorrhizal Without P. cinnamoni	Nonmycorrhizal With P. cinnamoni	Mycorrhizal with Pisolithus tinctorius Without P. cinnamoni	Mycorrhizal with Pisolithus tinctorius With P. cinnamoni
Stem dry wt. (mg)	99	81	185	203
Root dry wt. (mg)	124	86	131	134
Lateral roots	22	10	23	21

(c) Increased Host Resistance to Drought and Extreme Soil Temperature. The ecological diversity of the specific mycorrhizal association can best be demonstrated under conditions of marked environmental change and stress. Marx and Bryan (8) subjected nonmycorrhizal and mycorrhizal loblolly pine seedlings to temperatures in excess of 45°C. *Pisolithus tinctorius* was the fungal symbiont in this study. They reported that 90% of the mycorrhizal seedlings survived, whereas only 45% of the nonmycorrhizal plants survived. Safir *et al.* (14) demonstrated that endomycorrhiza enhanced water uptake and transport in soybeans, thus improving the drought tolerance of these plants. The reduced moisture stress is a combination of improved nutrient status and expanded root system utilizing a greater soil volume.

From the preceding discussion and examples, it is apparent that the mycorrhizal association, which includes a specific plant and a specific fungi, has a unique set of ecological capabilities that dictates that the association be considered only as a unit. If this is done, we may be able to develop plants more able to adapt to different environmental stresses.

FACTORS INFLUENCING MYCORRHIZAE FORMATION

The advantages of this association can be obtained only if mycorrhizal root formation occurs. As a very general rule, conditions that allow optimal growth and balanced plant metabolic process will produce the largest quantity of mycorrhizal root. An imbalance in the many factors controlling plant metabolism will reduce intensity of mycorrhizal formation.

The fungal symbiont obtains much of the organic material required for growth from the host plant (19). As a result, it is logical to expect that full sunlight, which allows for maximum photosynthetic rate, will maintain high levels of mycorrhizal root formation (4). A second requirement for maximum mycorrhizal root formation is an adequate supply of soil moisture. Care must be taken to prevent excess buildup because the fungal symbiont is an obligate aerobe. Under the conditions which develop as a result of flooding, the association will be destroyed (2).

Nutrient levels must be adequate for good plant growth to obtain maximum mycorrhizal formation. Lister *et al.* (6) demonstrated this after examining mycorrhizal formation in white pine under a varying combination of nitrogen and phosphorous levels (Table 3). Sinclair (16) indicated that the nutritional effect on formation frequency will vary for different mycorrhizal formers. In his study, he noted fewer tomentose mycorrhizae on 20-week-old seedlings that had received 200 KgN/ha than on unfertilized or superphosphate fertilized (200KgP/ha) plants. With the smooth ectomycorrhizal forms, no difference in frequency of occurrence was

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noted under the three different nutritional regimes (unfertilized, 200 KgN/ha and 200 KgP/ha).

Table 3. Effects of various levels of nitrogen and phosphorous on mycorrhizal abundance (arbitrary units) in P. strobus L. seedlings

N (mg/l)	P (mg/l)		
	0	173	692
0	−	+ +	+ +
2.5	−	+ + + +	+ +
53	+	+ + +	+
265	+	0	0

PRACTICAL CONSIDERATIONS

Certainly the potential exists for a beneficial growth response from controlling the specific mycorrhizal former. This is probably best demonstrated by work of Theodorou and Bowen (21) which is summarized in Table 4.

Table 4. Response of Pinus radiata to different mycorrhiza.

Inoculum	Height[1] (cm)
Suillus granulatus	482
Rhizopogon luteolus	454
Suillus luteus	414
Uninoculated	334

LSD	40	P = 0.05
	58	P = 0.01

[1]Mean of 27 trees 60 months after planting.

The different levels of growth stimulation produced by the different fungal symbionts should be noted. It has further been demonstrated (5) that the effect of a given inoculum will vary as the outplanting site is changed.

With this in mind, is it possible to manipulate the associated mycorrhizal flora at the practical level? In many nursery operations, sterilization of seed buds is a necessary practice to control fungal pathogens, nematodes and weeds. Sinclair (15) stated "Potential opportunities for manipulating mycorrhizal fungi in previously fumigated soil exist during the first several weeks of seedling growth, before indigenous fungal symbionts extensively colonize the root systems". Nursery soil could therefore be inoculated but at present there are no proven practices available. A few government and private nurseries in the Southeastern U.S.A. are in the initial stages of carrying out large-scale inoculation of loblolly pine with a selected symbiont, Pisolithus tinctorius (Marx, per. comm.). They will be using a basidiospore inoculum. At present, there are few fungal species where an adequate number of spores could be collected for such a large-scale nursery operation.

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Because of the lack of suitable quantities of inoculum for nursery bed application, the container production system offers the greatest opportunity for selected mycorrhizal manipulation. A much smaller volume of soil must be sterilized and re-inoculated, hence the associated costs of providing inoculum in high densities are reduced. The inoculum required for such a program can be grown on an artificial nutrient medium added to a peat-vermiculite carrier mix (9) or on a variety of cereal grains (12). This material can be easily incorporated within the container soil mix to provide a high density of selected inoculum.

Nevertheless, the problems must not be underestimated. Any inoculation hastily executed is bound to fail. Such failures will serve only to discredit a potentially effective technique. Accordingly, before a decision is made to inoculate a large number of plants, we must select the appropriate fungal stock, determine the best time for inoculation, establish optimal conditions for the development of the organism and the association, and develop adequate test methodology.

The mycorrhizal association has developed through a long period of selective ecological pressures and is now an important feature of the adaptation of plants to a range of natural sites. Failure to take advantage of such a symbiotic association will result in the use of increasing quantities of fertilizers and pesticides without an appropriate return in quality of plant produced, if the ability to establish on and utilize a natural site is the accepted quality standard.

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